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FIELDIANA: GEOLOGY

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GEOLOGICAL SERIES

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VOLUME 20



FIELD MUSEUM OF NATURAL HISTORY
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Revised Classification of Pteraspididae with Description of New Forms from Wyoming

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CURATOR OF FOSSIL FISHES

FIELD MUSEUM OF NATURAL HISTORY

In 1967 in connection with the description of a new pteraspid from Utah, I reviewed and revised the classification of this family. Now, in studying extensive collections in Field Museum from the Bighorn Mountains of Wyoming, I have felt the necessity to review this classification again, and particularly to re-evaluate the characters which have been used to distinguish genera and species. The classification that I have arrived at is essentially the same as that of my 1967 paper, and I will repeat it with minor changes, additions, and further justifications. My own studies have been largely restricted to North American material, and so I have attempted no detailed review of European forms. Most of the additions concern the genus *Protaspis* and its relatives, which are the common pteraspids of the western United States. Important new information about the structure of these forms has been provided by the material from the Bighorn Mountains of Wyoming, and by a restudy of old material from Utah and from Beartooth Butte, Wyoming. I have included all of the genera in one family, Pteraspididae, and feel no need to elevate it to the rank of suborder or order, as did Tarlo (1962, p. 265), Obruchev (1964, p. 63), and Stensiö (1964, p. 361), although this is necessary if *Doryaspis* is placed in a family of its own. As stated below, I feel that the purposes of classification are satisfied equally well by isolating *Doryaspis* from other pteraspids in a separate subfamily, which requires only the use of another subfamily, Pteraspidinae, to include typical pteraspids.

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I have given particular attention in this study to the structure of the branchial openings and the rostral plate. In the classifications of Stensiö (1958, 1964) and Tarlo (1961), the rostral structure has been used as the primary character for distinguishing genera. Among the pteraspids from the western United States there are also important differences in the rostrum, yet, in spite of this, I feel that the majority of the species are closely related, as indicated by their broad, highly vaulted dorsal shields, posterior branchial openings, and usually scale-like dorsal spines. This suggests that many rostral characters have been independently acquired in the American species as a result of an evolution paralleling that found in Europe. For this reason I have given the rostral characters less weight, and have, for example, included in the subgenus *Protaspis* species with rostra sufficiently different to distinguish the genera of Stensiö and Tarlo. The posterior branchial openings, which particularly characterize *Protaspis*, occur in certain European species. I have not studied these forms, so cannot come to any definite conclusions as to whether they are closely related to American species or the result of parallel evolution. For this reason I have provisionally kept them subgenerically distinct.

Specimens whose catalogue numbers have the prefix PF are in the collection of Field Museum of Natural History. The drawings have been made by Museum staff artist, Dr. Tibor Perenyi, many from my sketches.

Family Pteraspididae

Dorsal shield composed of rostral and pineal plates, a dorsal disc with a dorsal spine attached to its posterior part, as well as paired orbital, branchial, and cornual plates, the latter occasionally reduced, absent, or two pairs. Ventral shield formed by a large ventral disc, variably developed paired lateral, oral, and sometimes postoral plates, and in *Doryaspis* a pseudorostrum. Branchial openings more or less posteriorly placed at or near the lateral margins of the dorsal shield, typically at the posterior ends of the branchial plates, and commonly bounded posteriorly by cornual plates. Two or three pairs of sensory canals radiate from the center of ossification of the dorsal disc. Plates and scales consist of a tangentially laminated basal layer attaining only moderate thickness, a middle layer characterized by relatively large chambers, and a superficial layer consisting of narrow dentine ridges, or in some forms of tubercles.

Subfamily Pteraspidinae

Rostral plate extending anteriorly over the mouth; no pseudo-rostrum attached to the ventral shield.

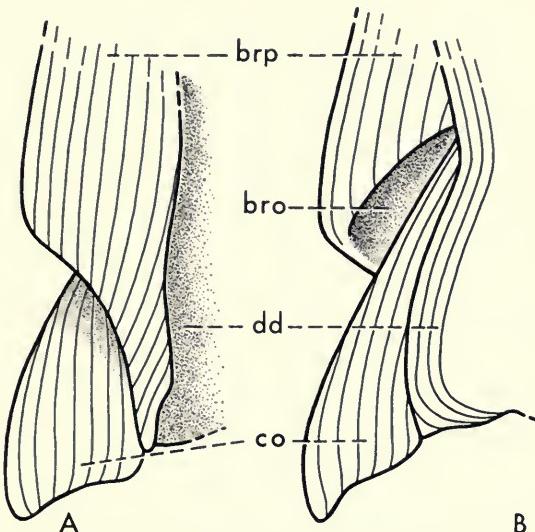


FIG. 1. Region of branchial opening of *Protopteraspis primaeva* (Kiaer), based largely on PF 1078 ($\times 7$). A, ventral view, right side; B, dorsal view, left side. bro, branchial opening; brp, branchial plate; co, cornual plate; dd, dorsal disc.

Protopteraspis Leriche, 1924

Type species.—*Protopteraspis gosseleti* Leriche.

Protopteraspis Leriche, 1924, Bull. Soc. Belge Géol., Pal., Hydr., 33, p. 149 (footnote), (subgenus of *Pteraspis*).

Simopteraspis White, 1950, Bull. Brit. Mus. (Nat. Hist.), Geol., 1, p. 76 (subgenus of *Pteraspis*).

Zascinaspis Stensiö, 1958, Traité de Zool., 13, fasc. 1, p. 255; Tarlo, 1961, Acta Palaeont. Polonica, 6, pp. 378–379.

Diagnosis.—Small to medium-sized pteraspids. The rostrum short and bluntly rounded, with its ventral preoral surface short and lacking a preoral field.¹ Branchial openings well in advance of the postero-lateral corners of the dorsal shield, and bounded by branchial and cornual plates (fig. 1).

¹I have adopted the following terminology for the ventral surface of the rostrum: *Ventral preoral surface*, the entire ventral surface of the rostrum anterior to the mouth, and including in some genera the *preoral field*, a clearly defined area elevated above the rest of the rostral surface and lacking ornamentation of dentine ridges; and the *ascending lamella*, the posterior part of the ventral preoral surface which rises dorsally anterior to the mouth.

Discussion.—Although in 1967 I followed Leriche and White in ranking this as a subgenus, I now feel warranted in elevating it (as well as subgenera *Pteraspis* and *Althaspis*) to generic rank. White (1961, pp. 257–258) prefers to use *Simopteraspis*, and to retain *Protopteraspis* for *P. gosseleti* alone because the preoral region of the latter is unknown. However, *P. gosseleti* and the type species of *Simopteraspis*, *Pteraspis leathensis*, are so similar in other respects that at one time White (1950, p. 82) believed that they might turn out to be conspecific, so I feel justified in placing them in the same genus.

The species referred to *Simopteraspis* by White in 1950 are small, primitive forms with blunt rostra and typical branchial openings (fig. 1). In addition, each has a small pineal plate isolated from the orbitals, lacks postoral plates, and has the posterior extensions of the supraorbital canals (pineal canals of Stensiö) forming a V-shaped loop on the dorsal disc. I refer also to *Protopteraspis* the species placed in *Zascinaspis* by Stensiö in 1958 and Tarlo in 1961 (*Brachiopteraspis heintzi* Brotzen, *B. grossi* Brotzen, and *Pteraspis carmani* Denison), which differ mainly in their larger size and in characters correlated with size, such as the relatively larger ventral preoral surfaces, and the wider pineal plates in contact with the orbitals. The presence of postoral plates in *P. carmani* may be related to size also. The extension of the supraorbital canals onto the dorsal disc is not known in the species referred to *Zascinaspis*, and may be characteristic only of small primitive species; it is retained in *Althaspis whitei* (Denison, 1955, fig. 110A), and in a modified form in one specimen of *Pteraspis rostrata* (White, 1935, fig. 68).

Pteraspis Kner, 1847

Type species.—*Cephalaspis rostratus* Agassiz.

Pteraspis Kner, 1847, Haidinger's Naturw. Abh., 1, p. 165.

Scaphaspis Lankester, 1865, Rept. Brit. Assoc. Adv. Sci., Trans. Sect., 1864, p. 58 (in part).

Podolaspis Zych, 1931, Fauna Ryb Dewonu i Downtonu Podola, p. 89.

Brachiopteraspis Brotzen, 1936, Ark. Zool., 28A, no. 22, pp. 31–35.

Mylopteraspis Stensiö, 1958, Traité de Zool., 13, fasc. 1, p. 255.

Parapteraspis Stensiö, 1958, Traité de Zool., 13, fasc. 1, p. 265.

Plesiopteraspis Stensiö, 1958, Traité de Zool., 13, fasc. 1, p. 265.

Diagnosis.—Moderate-sized pteraspids. The rostrum somewhat elongate and with a preoral field developed on at least the posterior part of its ventral preoral surface. Branchial openings well in ad-

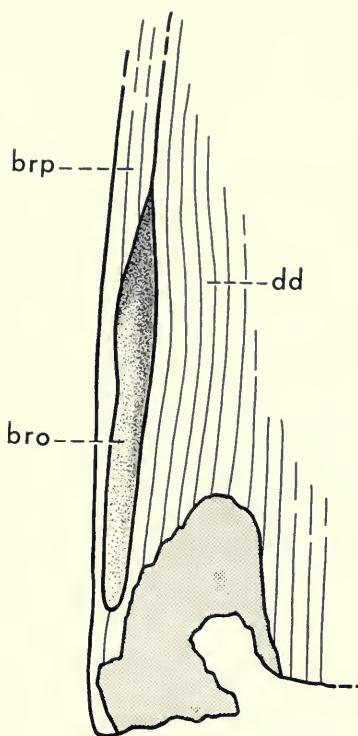


FIG. 2. Left branchial opening of *Pteraspis* ? *priscillae* (Denison), dorsal view, PF 867 ($\times 5$). *bro*, branchial opening; *brp*, branchial plate; *dd*, dorsal disc.

vance of the postero-lateral corners of the dorsal shield, and bounded by branchial and well-developed cornual plates.

Discussion.—As used here, the genus *Pteraspis* is restricted to the species referred to the subgenus *Pteraspis* in my 1967 paper. Its most important distinguishing feature is the presence on the ventral surface of the rostrum of a preoral field lacking dentine ridges and probably representing the locus of sensory organs. Its branchial openings are basically similar to those of *Proptopteraspis* (fig. 1).

White (1961, p. 270) has questioned the reference of *Protaspis priscillae* Denison (1953, pp. 348–349, figs. 82–83) to *Protaspis*. Further preparation and study of the type and only specimen has shown that he was correct, for there appear to be slender branchial openings (fig. 2, *bro*) well in advance of the posterior corners of the shield with the usual relations of those of *Pteraspis*, except that distinct cornual plates cannot be identified. Little of the ventral surface

of the rostrum can be seen, but there is a median unornamented area that is presumably a preoral field, so this species can be referred to *Pteraspis* or possibly to *Rhinopteraspis*. It shows resemblances to another elongate, slender species, *Pteraspis dewalquei* Fraipont, as figured by White (1960, fig. 3), though the ventral surface of the rostrum of the latter is unknown, and its generic reference is also uncertain.

Althaspis Zych, 1931

Type species.—*Pteraspis elongata* Zych (non Alth)=*Althaspis samsonowiczi* Tarlo.

Podolaspis (*Althaspis*) Zych, 1931, Fauna Ryb Dewonu i Downtonu Podola, p. 89.

Brotzenaspis Stensiö, 1958, Traité de Zool., 13, fasc. 1, pp. 265, 272.

Pseudopteraspis Stensiö, 1958, Traité de Zool., 13, fasc. 1, p. 254.

Pteraspis (*Cymripteraspis*) White, 1960, Bull. Inst. Roy. Sci. Nat. Belg., 36, no. 6, p. 8 (footnote).

Loricopteraspis Tarlo, 1961, Acta Palaeont. Polonica, 6, p. 382.

Diagnosis.—Mostly moderate-sized or rather large pteraspids. The rostrum more or less elongate, but lacking a preoral field, and

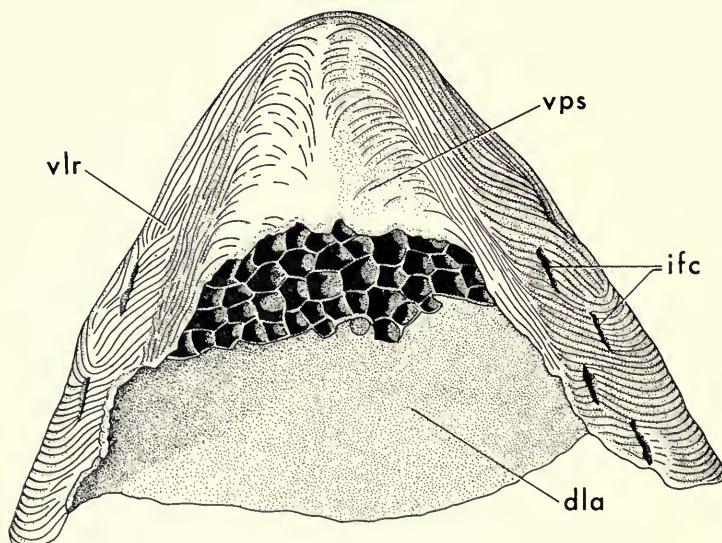


FIG. 3. Rostral plate of *Althaspis whitei* (Denison), ventral view, PF 1195 (× 6). *dla*, ventral surface of dorsal lamina, lacking basal layer and exposing cancelli anteriorly; *ifc*, pores of infraorbital canal; *vl̄r*, ventro-lateral face; *vps*, ventral preoral surface.

having its ventral preoral surface covered with dentine ridges. Branchial openings well in advance of the postero-lateral corners of the dorsal shield, and bounded by branchial and cornual plates.

Discussion.—An irregular dentine ridge arrangement on the ventral side of the rostrum was used by Tarlo (1961, p. 382) to distinguish *Loricopteraspis*, but this is hardly evidence that this area was formed of a number of separate synchromonomorial units as he assumed. *Pteraspis whitei* (Denison, 1955, p. 450–454) may show an irregular development of the ventral rostral ridges (fig. 3), though this is a small species with the rostrum only slightly elongate; it may be considered a primitive species of *Althaspis*.

White (*in Allen, Halstead, and Turner, 1968*, pp. 151–152) still maintains the generic or subgeneric distinction of *Cymripteraspis*, though this differs from typical *Althaspis* only in the presence of a small plate with concentric ridges on the preoral border. Halstead (*in Allen, Halstead, and Turner, 1968*, p. 145) has attempted to explain this as an oral plate appressed to the preoral border, an explanation denied by White. In any case, it appears at present to be a rather insecure basis for the erection of a distinct genus or subgenus.

Brotzenaspis pteraspidoides Stensiö (1958, fig. 152B) is a small form with a rostrum of only moderate length. Stensiö's figure shows the ventral surface of the rostrum to be covered with more or less transverse ridges, which indicates a relationship to *Althaspis*. Tarlo (1961, p. 378) referred it to *Zascinaspis* (*Proptopteraspis* of this paper), but that seems to be incorrect.

Rhinopteraspis Jaekel, 1919

Type species.—*Palaeoteuthis dunensis* Roemer, 1855.

(For synonymy, see Tarlo, 1961, pp. 368–370.)

Diagnosis.—Moderate-sized to large pteraspids. The rostrum much elongated, with a preoral field formed by a separate plate. Branchial openings in advance of the postero-lateral corners of the dorsal shield, but the cornual plates reduced or absent.

Discussion.—The International Commission on Zoological Nomenclature (1957, p. 43) placed *Rhinopteraspis* Jaekel on the official list, and rejected the earlier names, *Archaeoteuthis* Roemer and *Palaeoteuthis* Roemer, as invalid. The type species was designated as *Palaeoteuthis dunensis* Roemer, and it was also placed on the official list. Since this decision, Tarlo (1961, p. 370) has indicated that *Rhinopteraspis dunensis* is a synonym of the earlier name, *Stegano-*

dictyum cornubicum M'Coy, 1851, as already claimed by Lankester in 1868. Since *cornubicum* was the type species of *Steganodictyum*, strict adherence to the law of priority would require the use of M'Coy's name for the genus and species. However, *Steganodictyum* would appear to qualify as a *nomen oblitum*, as defined in Article 23b of the International Code of Zoological Nomenclature, though this is not true of the specific name. If Lankester and Tarlo are correct, we may then refer to the genus as *Rhinopteraspis*, and its best known species as *R. cornubica* (M'Coy), but the type species remains *Palaeotheuthis dunensis* Roemer, here accepted as a synonym of *R. cornubica*.

As I suggested in 1967 (p. 34), *Belgicaspis* Zych, whose type species is *Pteraspis crouchi* Lankester, may belong to *Rhinopteraspis* or be closely related. Its preoral field is formed by a separate plate, as indicated by White (1960, p. 8 footnote), its rostrum is long and slender, though variable in shape (White, 1961, pl. 36, figs. 4-11), and its cornual plates are reduced or absent. As noted above (p. 6), *Protaspis priscillae* Denison may belong to *Rhinopteraspis*.

Protaspis Bryant, 1933

Type species.—*Pteraspis bucheri* Bryant, 1932.

Diagnosis.—Moderate-sized to large pteraspids with the dorsal shield rather broad or highly vaulted. The rostrum very short to moderate in length, with the development of its ventral preoral surface dependent on the rostral length. The branchial plates long, the cornual plates reduced or absent, and the branchial openings at the postero-lateral corners of the shield. The dorsal spine usually small, recumbent, and scale-like.

Discussion.—*Glossoidaspis* Branson and Mehl, 1931 predates *Protaspis* Bryant, but was based only on a dorsal disc which shows no generically diagnostic characters, so it must remain *incertae sedis*.

As used here, the genus *Protaspis* is restricted to those species in which the branchial openings are at the postero-lateral corners of the shield. This requires the removal of certain species formerly referred to *Protaspis* in which the branchial openings have a more anterior position. I have not given the ventral preoral surface much weight in classifying *Protaspis* because its development is clearly related to the length of the rostrum. Thus, in species with a short, broad rostrum (figs. 14, 19) the ventral preoral surface is small, as in *Propteraspis*, while in species with longer rostra (fig. 9) the ventral preoral surface may be considerable and a preoral field may be developed, as in *Pteraspis*. The genus *Protaspis* has been subdivided into

a number of subgenera, based largely on differences in ornamentation, on details of the structure of the external gill openings, and, in one case, on the aberrant development of the dorsal spine and orbital plates.

Subgenus *Protaspis* Bryant, 1933

Type species.—*Pteraspis bucheri* Bryant, 1932.

Diagnosis.—Dorsal shield of moderate breadth. Ornamentation consisting of ridges of dentine arranged approximately parallel to lines of growth. Branchial openings facing posteriorly or postero-dorsally, and bounded externally by the branchial plates and sometimes by the dorsal disc, with cornual plates absent or poorly developed.

Protaspis (Protaspis) bucheri (Bryant), 1932

Pteraspis bucheri Bryant, 1932, Proc. Amer. Phil. Soc., 71, pp. 232–238, text-fig. 1; pl. 1; pl. 2, fig. 1; pl. 3, figs. 1–2.

Protaspis bucheri Bryant, 1933, Proc. Amer. Phil. Soc., 72, pp. 294–296, text-fig. 1A; pl. 1; pl. 2, figs. 1–2; pl. 5, fig. 1; 1934, Proc. Amer. Phil. Soc., 73, p. 152, pl. 22; pl. 26, fig. 2; 1935, Proc. Amer. Phil. Soc., 75, p. 122, pl. 13, fig. 1; White, 1935, Phil. Trans. Roy. Soc. London (B), 225, p. 438; Denison, 1953, Fieldiana: Geol., 11, p. 334.

Protaspis brevirostris Bryant, 1933, Proc. Amer. Phil. Soc., 72, pp. 297–298, pl. 8, figs. 1–2; 1935, Proc. Amer. Phil. Soc., 75, p. 123, pl. 15; Denison, 1953, Fieldiana: Geol., 11, p. 334.

Occurrence.—Lower Devonian, Beartooth Butte formation, Beartooth Butte, Park County, Wyoming.

Diagnosis.—Rostrum short ($RL/TL=0.11-0.19$)¹ and broadly rounded anteriorly. Ornamentation coarse with 4.5 to 6.5 ridges per millimeter.

Discussion.—Certain of Bryant's figures (1932, pl. 1; 1933, pl. 1; 1935, pl. 15), as well as one specimen in Field Museum (PF 2168), show that the branchial plates extend to the postero-lateral corners of the dorsal shield, where they are simply terminated and usually truncate. The branchial openings must have been at their posterior ends.

¹ The measurements used in determining rostral ratios are: RL, length of rostral plate measured in the midline; RW, maximum width of rostral plate; and TL, total length of dorsal shield, measured in midline, but excluding the dorsal spine.



FIG. 4. Dorsal shield of type specimen of *Protaspis (Protaspis) megrewi*, n. sp., PF 4337 ($\times \frac{3}{4}$).

Protaspis (Protaspis) dorfi (Bryant), 1932

Pteraspis dorfi Bryant, 1932, Proc. Amer. Phil. Soc., **71**, pp. 238–240, text-fig. 3; pl. 2, fig. 2; pl. 4.

Protaspis dorfi Bryant, 1933, Proc. Amer. Phil. Soc., **72**, pp. 296–297, text-fig. 1B; pl. 3; pl. 5, fig. 2; pls. 6–7; 1934, Proc. Amer. Phil. Soc., **73**, pp. 152–153, pl. 23; pl. 24, fig. 1; Denison, 1953, Fieldiana: Geol., **11**, pp. 324, 334, fig. 74.

Occurrence.—Lower Devonian, Beartooth Butte formation, Beartooth Butte, Park County, Wyoming.

Diagnosis.—Rostrum short ($RL/TL=0.14-0.18$) and narrowly rounded anteriorly. Ornamentation very fine with 8 to 12 ridges per millimeter.

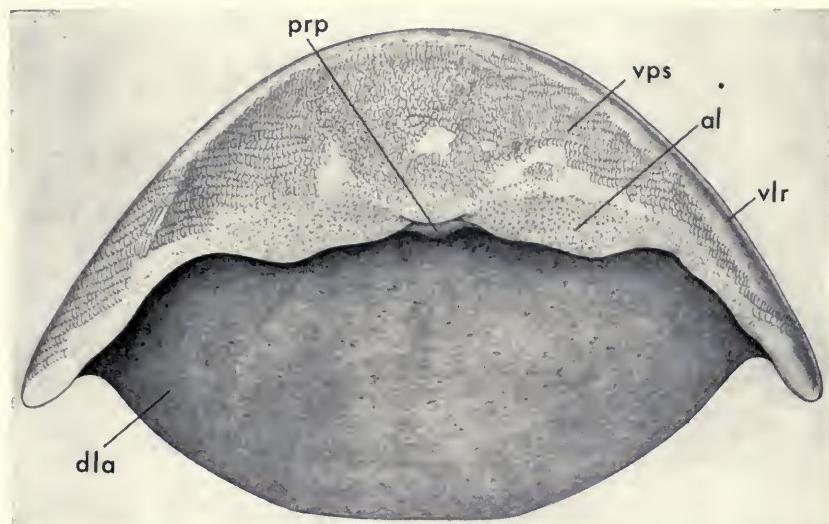


FIG. 5. Rostral plate of *Protaspis (Protaspis) mcgrewi*, n. sp., ventral view restored from PF 4763 (about $\times 2$). *al*, ascending lamella; *dla*, ventral surface of dorsal lamina; *prp*, median preoral wall; *vlr*, ventro-lateral face; *vps*, ventral preoral surface.

Discussion.—Bryant's figure of the type specimen (1932, pl. 4) indicates that the branchial plates and openings were developed as in *Protaspis bucheri*.

Protaspis (Protaspis) mcgrewi,¹ new species

Type.—Field Museum, PF 4387, a dorsal shield, complete except for its right postero-lateral corner (figs. 4, 6A, 7A).

Referred specimens.—Dorsal shields, PF 4758–9, 4763 (figs. 5, 6B), 4914, 4917, 4356, and part of 4911; incomplete juvenile dorsal shield, PF 4491; ventral disc, PF 4361; rostral plates, PF 5265, 5267, 5269, 5278, 5284–5, 5288, 5295.

Occurrence.—Lower Devonian, Beartooth Butte formation, Cottonwood Canyon, east of Lovell, NE $\frac{1}{4}$, sec. 4, T56N, R93W, Big-horn County, Wyoming.

Diagnosis.—Dorsal shield broader or more highly vaulted than in *P. bucheri* and *P. dorfi*. Rostrum of moderate length and broadly rounded anteriorly, longer relatively than in *P. bucheri* or *P. dorfi*.

¹ After Dr. Paul O. McGrew who first called my attention to the rich occurrence of fossil fishes in Cottonwood Canyon.

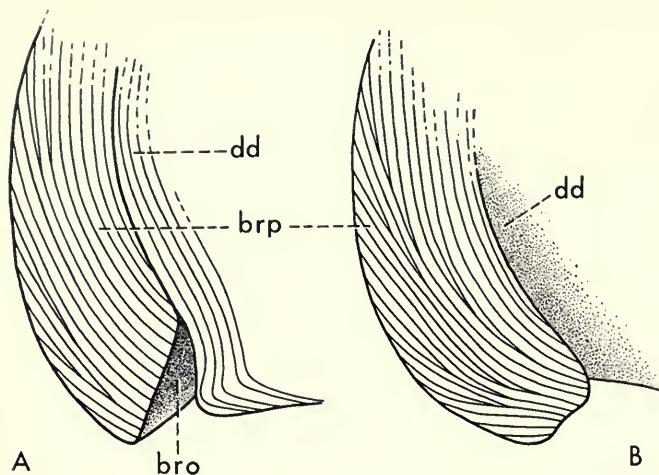


FIG. 6. Region of branchial opening of *Protaspis (Protaspis) mcgrewi*, n. sp. (about $\times 1$). A, dorsal view of PF 4337; B, ventral view of PF 4763. *bro*, branchial opening; *brp*, branchial plate; *dd*, dorsal disc.

($RL/TL = 0.22-0.23$). Dorsal spine relatively long and projecting. Ornamentation coarse with about 5.5 ridges per millimeter in the midline of the dorsal disc. Length of the dorsal disc (excluding the dorsal spine) as much as 137 millimeters.

Description.—The dentine ridges (fig. 7A) typically have a smooth, gently convex crest, but locally may be flat-crested or tuberculate. There is a tendency for them to be grouped in bands separated by what are probably growth lines, and in some bands the ridges may be irregularly arranged, or rarely transverse or diagonal within the bands. In the central area of the dorsal disc the ridges, where unworn, are finer, more convex, tuberculate, and with crenulate margins. The rostrum has a well-developed ventral preoral surface (fig. 5, *vps*), covered medially with short to elongate, crested dentine ridges with prominent lateral projections, reminiscent of those of *Traquairaspis*; this area is bounded laterally by borders with relatively broad dentine ridges, or in the figured specimen, with bands of transverse or diagonal ridges similar to those of subgenus *Cosmaspis*. Ascending lamellae mark the posterior edge of the ventral preoral surface, while medially there is a preoral wall (fig. 5, *prp*) connecting the ventral preoral surface with the dorsal lamina of the rostral plate; this structure will be described more fully in *Protaspis (Protaspis) brevispina*. The pineal plate usually contacts the orbitals, and distinct suborbital plates are probably not present below the orbitals.

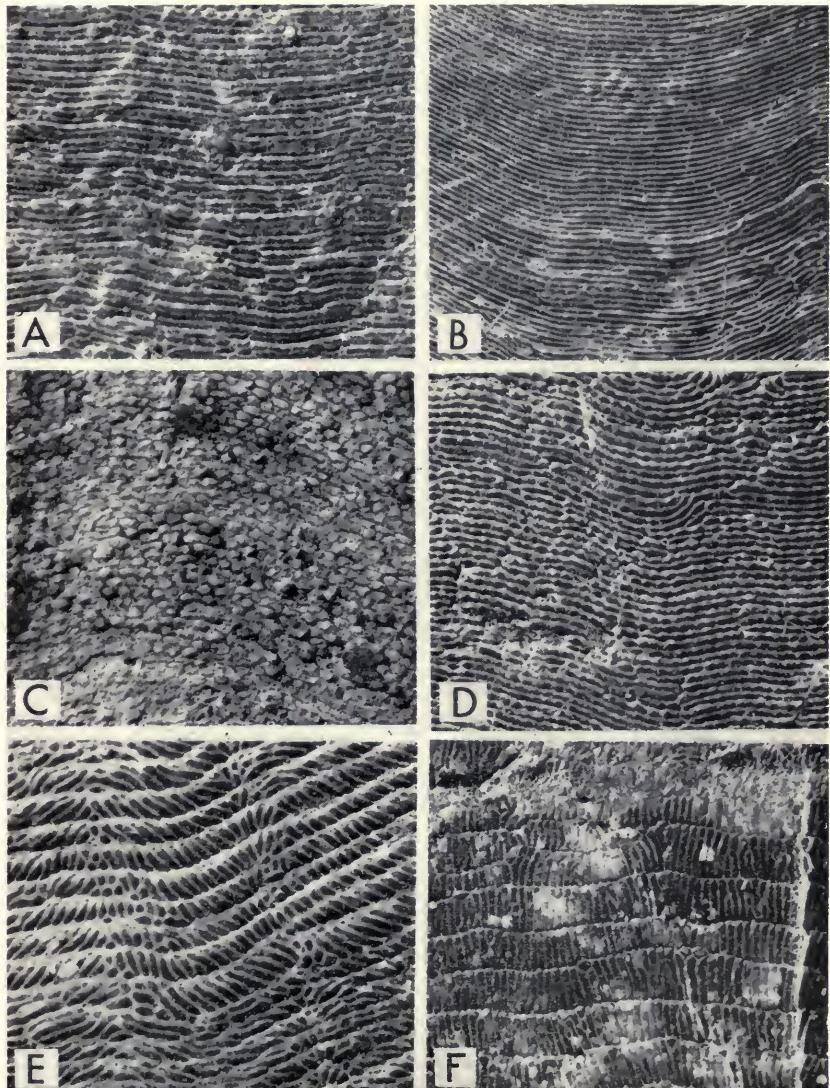


FIG. 7. Ornament of dorsal shield ($\times 6$). A, *P. (Protaspis) mcgrewi*, n. sp., PF 4337; B, *P. (Protaspis) brevispina*, n. sp., PF 4343; C, *P. (Cyrtaspidichthys) ovata* (Bryant), PF 1523; D, *Lampraspis tuberculata*, n. sp., PF 4913; E, *P. (Cosmaspis) transversa*, n. sp., PF 4334; F, *P. (Cosmaspis)* sp., PF 951.

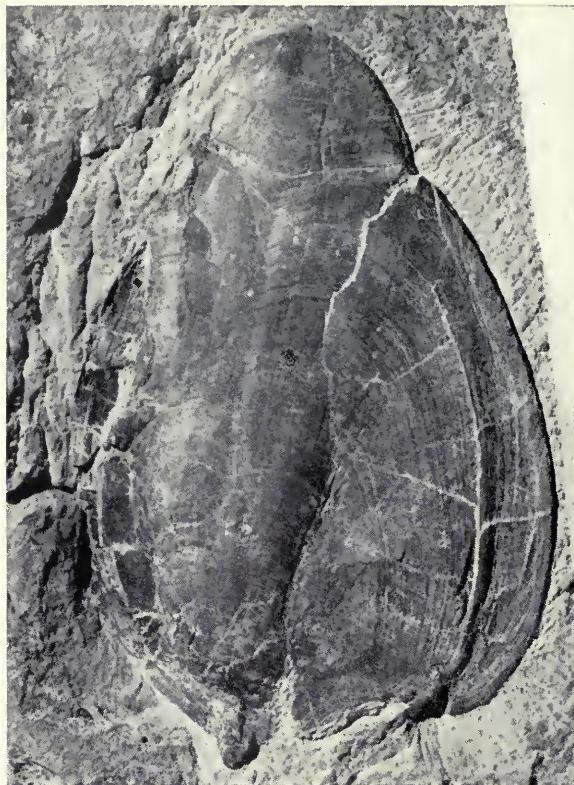


FIG. 8. Dorsal shield of type specimen of *Protaspis (Protaspis) brevispina*, n. sp., PF 4343 ($\times \frac{3}{4}$).

and between the rostral and branchial plates. In all specimens the postero-lateral corners of the dorsal disc form the medial margins of the branchial openings, which are directed postero-medio-dorsally (fig. 6, bro).

Protaspis mcgrewi resembles *P. bucheri* in its ornament and rostral shape, but differs in its broader (or more vaulted) dorsal shield, in the greater length of the rostrum, and possibly in the greater length of the dorsal spine. Its closest relative is *Protaspis (Cosmaspis) transversa* (p. 21), which it resembles in many features, most especially in the occasional occurrence of bands of transverse or diagonal ridges. However, this is rare in *mcgrewi*, but characteristic of *transversa*, which also differs distinctly in the structure of its branchial openings.

Protaspis (Protaspis) brevispina, new species

Type.—Field Museum, PF 4343, a dorsal shield crushed on the left side (figs. 7B, 8, 11A).

Referred specimens.—Dorsal shields, PF 4340, 4344, 4346–8, 4352, 4762, 4764, 4766, 4768, 4770, 4910, 4912, 4918, 4929–30, 4933–5, 4940; associated dorsal and ventral discs, PF 4345, 4365, 4923; dorsal discs, PF 4372, 4388, 4937, 4939, 4986–7, 4989, 4991, 4999, 5062; ventral discs, PF 4360, 4368, 4779, 4785, 4947; rostral plates, PF 5274 (fig. 10A), 5279–80, 5296 (fig. 10B–C), 5298, 5299 (fig. 9); branchial plates, PF 4376–7, 4380–1, 5314, 5322 (fig. 11B); incomplete articulated juvenile individual, PF 4959.

Occurrence.—Lower Devonian, Beartooth Butte formation, Cottonwood Canyon, east of Lovell, NE $\frac{1}{4}$, sec. 4, T56N, R93W, Big-horn County, Wyoming.

Diagnosis.—Shield moderately slender. Rostrum of moderate length ($RL/TL=0.20-0.24$), narrowly rounded anteriorly, and with a well-developed preoral field covered with a fine reticular ornament.

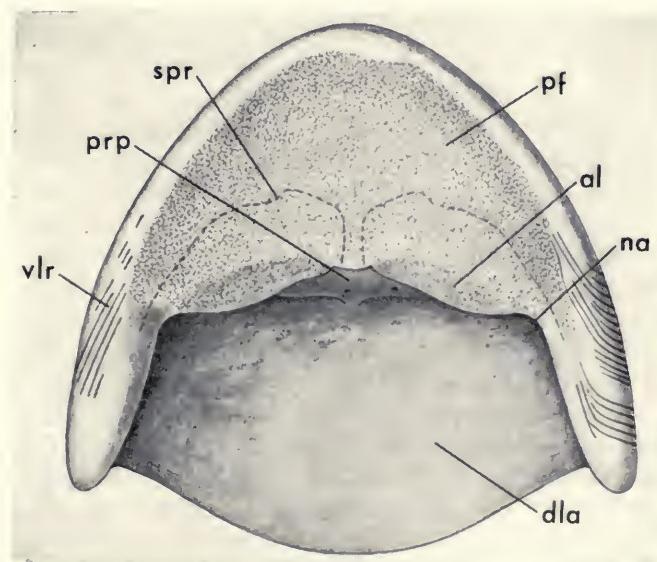


FIG. 9. Rostral plate of *Protaspis (Protaspis) brevispina*, n. sp., ventral view, restored largely from PF 5299 ($\times 2\frac{1}{4}$). *al*, ascending lamella; *dla*, ventral surface of dorsal lamina; *na*, possible narial notch; *pf*, preoral field; *prp*, median preoral wall; *spr*, outline of paired rostral space, based on dissection of PF 5298; *vlr*, ventro-lateral face.

Dorsal spine short, projecting little or not at all. Ornament rather fine with 6 to 8 ridges per millimeter near the midline of the dorsal disc. Dorsal shield estimated to have attained a length of 175 millimeters.

Description.—This species differs from *P. megrewi* in its narrower proportions, longer and more narrowly rounded rostrum, short dorsal spine, and usually by its finer dentine ridges. From *P. dorfi* it may be distinguished by its coarser ridges and relatively longer rostrum.

The more or less complete dorsal shields referred to this species have a length of 107–142 millimeters. The largest specimen referred here, PF 4365, is estimated to have had a dorsal shield 175 millimeters long on the basis of the length of its ventral disc, which is 140 millimeters. The dentine ridges (fig. 7B) are usually smooth with flat or gently convex crowns and crenulate margins, but in some specimens the crests may be slightly tuberculate. Near the center of the dorsal disc the ridges may be similar, but sometimes their crests are cut by cross grooves which give the ridges the appearance of a row of overlapping pointed scales.

The rostrum is somewhat variable in shape and proportions, but ventrally has a long preoral surface (fig. 9, *pf*) with fine reticular, probably non-dentinous ornament, comparable to the preoral field of *Pteraspis*. The posterior edge of the preoral field has a slight, rounded median process, bounded on either side by an ascending lamella (fig. 9, *al*). In many specimens there is a rostral space (fig. 10C, *spr*), widely open posteriorly, between the dorsal and ventral laminae of the rostrum. This is the usual condition in pteraspids with somewhat elongate rostra, and has been figured by Stensiö (1964, figs. 46B–C, 91A–C). In other specimens of *Protaspis brevispina*, especially PF 5299, there is a nearly vertical preoral wall (fig. 9, *prp*) in the midline at the posterior edge of the ventral lamina of the rostrum, and connecting it with the dorsal lamina. A longitudinal section of another specimen (PF 5274) shows that in the midline where the preoral wall is developed (fig. 10A, *prp*), the rostral space is absent and the rostrum is filled with spongy bone. On either side of the preoral wall the rostral space is present (fig. 10B, *spr*); its extent has been determined by dissection of another specimen (PF 5298) and indicated on Figure 9 (*spr*). This is important in the interpretation of pteraspid structure since it indicates the presence of a pair of pockets extending anteriorly from the oral cavity, and occupied in life by paired structures. These structures were probably nasal sacs, and they could have opened posteriorly into the

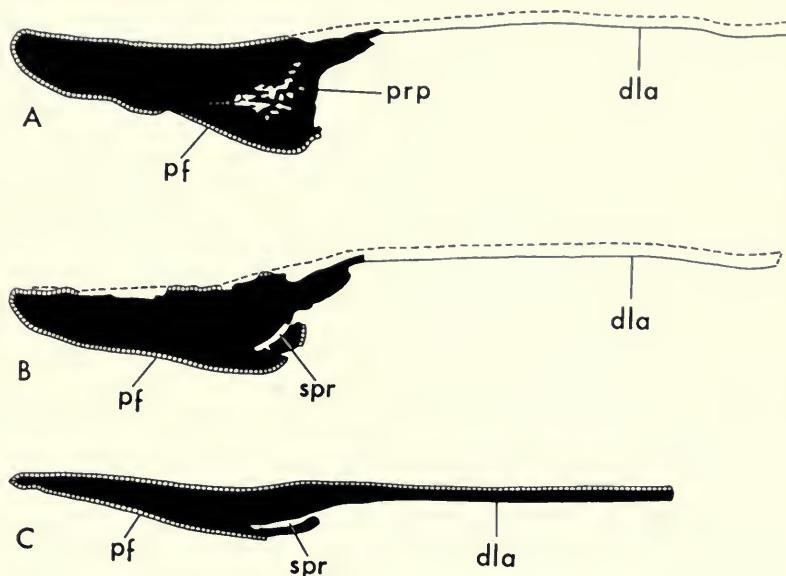


FIG. 10. Vertical longitudinal sections through rostral plates of *Protaspis* (*Protaspis*) *brevispina*, n. sp. ($\times 3$). A, sagittal section of PF 5274; B, parasagittal section of same rostrum; C, approximately sagittal section of PF 5296. *dla*, dorsal lamina; *pf*, preoral field; *prp*, median preoral wall; *spr*, rostral space.

buccal cavity, or perhaps postero-laterally to the exterior at the corners of the mouth, where notches are sometimes seen in the rostral plate (figs. 9, 19, *na*). A preoral wall has also been found in *Protaspis* (*Protaspis*) *mcgrewi* and *Protaspis* (*Cosmaspis*) *transversa*. Its absence in other species and in some specimens of *Protaspis* *brevispina* suggests that it formed only at maturity, perhaps as a part of the rostral plate itself, or perhaps as a distinct plate.

The pineal plate of *Protaspis* *brevispina* contacts the orbitals, and usually there are separate suborbital plates separating the branchial and rostral plates. The branchial openings (fig. 11, *bro*) are similar to those of *P. mcgrewi* with their medial margins formed dorsally by the postero-lateral corners of the dorsal disc. Below this, one or more small platelets, possibly cornuals (fig. 11, ? *co*), line the medial side of the branchial duct in some specimens.

Subgenus *Europrotaspis* White, 1961

Type species.—*Protaspis* (*Europrotaspis*) *crenulata* White, 1961.

Europrotaspis White, 1961, Bull. Brit. Mus. (Nat. Hist.), Geol., 5, pp. 268-270 (new subgenus).

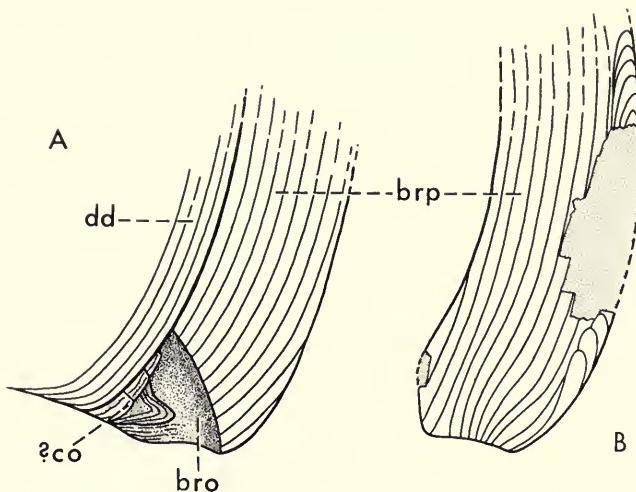


FIG. 11. Region of external branchial opening of *Protaspis (Protaspis) brevispina*, n. sp. (about $\times 2$). A, dorsal view, PF 4343; B, ventral view, PF 5322. bro, branchial opening; brp, branchial plate; ? co, possible cornual plates; dd, dorsal disc.

Diagnosis.—Similar to subgenus *Protaspis* except that each branchial opening is bounded medially by a small narrow cornual plate at the postero-lateral corners of the dorsal disc.

Discussion.—When White (1961, p. 268) erected the subgenus *Europrotaspis*, the structure of the branchial openings of the typical *Protaspis* was unknown. It now appears that the branchial openings are very similar in the two subgenera. In typical *Protaspis*, where cornual plates are known, they are small elements lying in the medial walls of the posterior ends of the branchial ducts, but they do not appear on the dorsal surface of the shield. In *Europrotaspis* (fig. 12, co), especially in *P. (Europrotaspis) arnelli* from Podolia (Brotzen, 1936, fig. 3), they differ only in extending to the dorsal surface of the shield, where they lie against the postero-lateral corners of the dorsal disc and form the medial edges of the branchial openings.

White used other characters to distinguish *Europrotaspis*. One was the large, flat preoral field of *P. (Europrotaspis) crenulata*, which he contrasted with the very narrow ventral preoral surface of “*Protaspis cf. bucheri*” (of Denison, 1953, fig. 78, here referred on p. 29 to *Oreaspis dunklei* n. gen., n. sp.). However, a well-developed preoral field may occur in those species of *Protaspis* which have a rostrum of moderate length, as *P. brevispina* (fig. 9). White also mentions the very large ridge scales of *Europrotaspis*, but all of his scales are

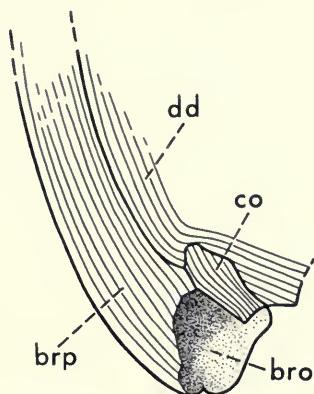


FIG. 12. Region of external branchial opening of *Protaspis (Europrotaspis) crenulata* White, after White, 1961. *bro*, branchial opening; *brp*, branchial plate; *co*, cornual plate; *dd*, dorsal disc.

isolated and their relative size uncertain; moreover, the ridge scales of *Protaspis dorfi* and *P. (Cosmaspis) transversa* are known to be relatively large. The asymmetrical ridge scales of *P. (Europrotaspis) crenulata* described by White can hardly be accepted as sufficient evidence for the presence of lateral keels, for they are isolated, and lateral keels are unknown in other pteraspids.

I conclude that *Europrotaspis*, as far as it is known, differs only in minor ways from the subgenus *Protaspis*.

Subgenus *Gigantaspis* N. Heintz, 1962

Type species.—*Gigantaspis isachseni* N. Heintz, 1962.

Giganthaspis A. Heintz, 1937, Skr. Svalbard og Ishavet, nr. 72, p. 18 (*nomen nudum*); Føyn and Heintz, 1943, Skr. Svalbard og Ishavet, nr. 85, p. 14 (*nomen nudum*); Dineley, 1960, Geol. Mag., 97, pp. 18, 20, 22–23, 30 (*nomen nudum*).

Gigantaspis N. Heintz, 1962, Norsk Polarinst., Årbok 1960, pp. 23–24.

Diagnosis.—Similar to the subgenus *Protaspis*, from which it is distinguished by the very slight vaulting of the dorsal disc, the upright dorsal spine, the relatively longer rostral plate, and by the slit-like branchial openings facing upward between the posterior ends of the branchial plates and the dorsal disc.

Discussion.—*Gigantaspis*, the characteristic pteraspid of the Kapp Kjeldsen division of the Wood Bay series of Spitsbergen, was recognized as a close relative of *Protaspis* by N. Heintz. She gave it generic rank, but I find that it fits well in the genus *Protaspis* as used

here, and differs from the subgenus *Protaspis* only in relatively minor characters that certainly warrant no more than subgeneric distinction. The branchial openings are fundamentally the same in both subgenera; in both there are no visible cornual plates (except possibly for small platelets in *Protaspis brevispina*), but in *Gigantaspis* the openings face more dorsally and are more slit-like. The dentine ridges of subgenus *Protaspis* may be "fine, smooth and entire," as described for *Gigantaspis*. The rostral plate is relatively longer than in any known species of subgenus *Protaspis*; based on the restoration of *P. (Gigantaspis) bocki* (N. Heintz, 1962, fig. 1A), $RL/TL=0.30$, compared to 0.11 to 0.24 in species of subgenus *Protaspis*. An upright dorsal spine is unknown in subgenus *Protaspis*, though it occurs in *Eucyclaspis* and doubtfully in *P. (Europrotaspis) arnelli*.

Subgenus *Cyrtaspidichthys* Whitley, 1940

Type species.—*Cyrtaspis ovatus* Bryant, 1932.

Cyrtaspis Bryant, 1932 (not of Fischer, 1853), Proc. Amer. Phil. Soc., 71, p. 241; 1933, Proc. Amer. Phil. Soc., 72, p. 304; White, 1935, Phil. Trans. Roy. Soc. London (B), 225, p. 438.

Cyrtaspidichthys Whitley, May 1940, Australian Nat., 10, p. 243; Denison, 1953, Fieldiana: Geol., 11, p. 318.

Eucyrtaspis White and Moy Thomas, June 1940, Ann. Mag. Nat. Hist. (11), 5, p. 507.

Diagnosis.—Dorsal shield broad or highly vaulted. Ornamentation consisting of oval dentine tubercles arranged in rows approximately parallel to the lines of growth (fig. 7C). Branchial openings directed postero-medially at the posterior ends of the branchial plates.

Protaspis (Cyrtaspidichthys) ovata (Bryant), 1932

Cyrtaspis ovatus Bryant 1932, Proc. Amer. Phil. Soc., 71, pp. 242–243, text-fig. 4, pl. 6, fig. 1; 1933, Proc. Amer. Phil. Soc., 72, pp. 304–305, text-fig. 5; pl. 5, fig. 3; pl. 14, figs. 1–2; 1935, Proc. Amer. Phil. Soc., 75, pp. 123–124, pl. 11, fig. 2, pl. 16.

Cyrtaspis papillatus Bryant, 1933, Proc. Amer. Phil. Soc., 72, p. 306, pl. 15, figs. 1–2; 1934, Proc. Amer. Phil. Soc., 73, pp. 153–154, pl. 25.

Cyrtaspis falcatus Bryant, 1933, Proc. Amer. Phil. Soc., 72, p. 307, pl. 17, fig. 1.

Protaspis (Cyrtaspidichthys) ovatus Denison, 1953, Fieldiana: Geol., 11, p. 336.

Occurrence.—Lower Devonian, Beartooth Butte formation, Beartooth Butte, Park County, Wyoming.

Diagnosis.—Shield very broad (or highly vaulted). Rostrum of moderate length ($RL/TL=0.25$ to 0.28) and rather sharply rounded anteriorly.

Discussion.—Specimens figured by Bryant (1933, pl. 14, fig. 2; 1935, pl. 16), as well as those in Field Museum (PF 1523, 1601, 2170), show that the branchial openings were fundamentally as in the subgenus *Protaspis*. The branchial plates are very broad and their posterior ends extend slightly beyond the postero-lateral corners of the dorsal disc, with the result that the branchial openings must have opened medially as well as posteriorly.

Protaspis (Cyrtaspidichthys) sculpta (Bryant), 1933

Cyrtaspis sculptus Bryant, 1933, Proc. Amer. Phil. Soc., 72, pp. 306–307, pl. 16, figs. 1–2.

Protaspis (Cyrtaspidichthys) sculptus Denison, 1953, Fieldiana: Geol., 11, p. 336.

Occurrence.—Lower Devonian, Beartooth Butte formation, Bear-tooth Butte, Park County, Wyoming.

Diagnosis.—Shield less broad (or less vaulted) than in *P. (C.) ovata*. Rostrum relatively shorter ($RL/TL = 0.20$) and bluntly rounded.

Subgenus **Cosmaspis**,¹ new subgenus

Type species.—*Protaspis (Cosmaspis) transversa*, new species.

Diagnosis.—Dorsal shield broad or highly vaulted. Ornamentation mostly arranged in bands more or less parallel to lines of growth, while within the bands the individual dentine ridges are arranged diagonally, or sometimes transversely or irregularly with respect to the bands. Branchial openings behind the dorsal disc at the posterior tips of the branchial plates.

Protaspis (Cosmaspis) transversa, new species

Type.—Field Museum, PF 4334, a nearly complete dorsal shield (figs. 7E, 13, 16).

Referred specimens.—Dorsal shields, PF 4335–6, 4338–9, 4349, part of 4352 (fig. 15), 4355, 4755, 4757, 4760, 4915, 4924, 4926, 4931–2, 4944, 5497; dorsal discs (juvenile), PF 4375, 4394, 4403, 4408, 4412, 4416, 4772–4, 4974, 4977, 4981, 4984, 5020, 5050–1, 5059, 5077; ventral discs, PF 4362–3, 4780, 4936; ventral discs (juvenile), PF 4450–1, 4453–4, 4486, 4994, 5016, 5122, 5148–9, 5175, 5177–8, 5180, 5184; dorsal and ventral discs, PF 4369; rostral plates, PF 4942, 5262, 5268, 5276–7, 5281 (fig. 14), 5291–4; orbital plates, PF 5211,

¹ From *κοσμος*, ornament; and *σπισ*, shield.

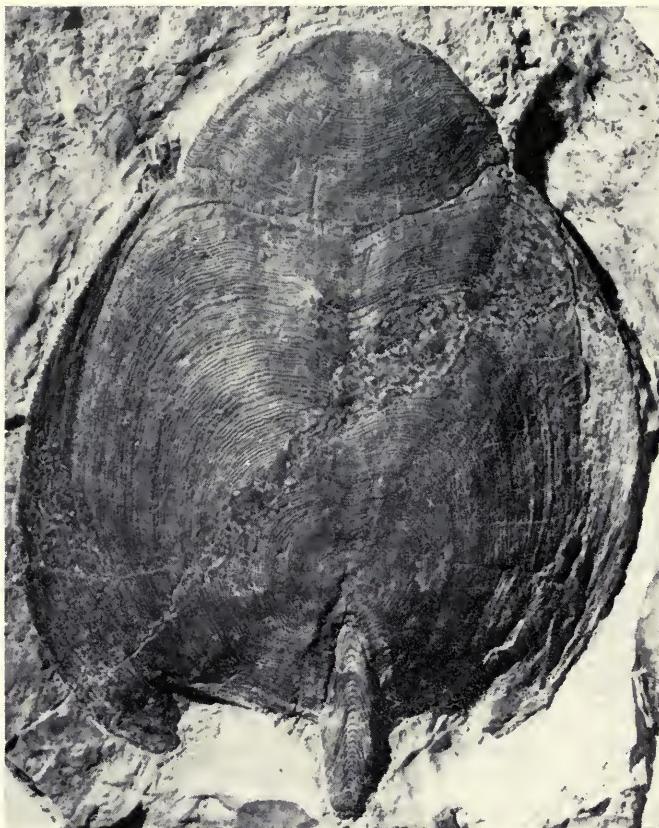


FIG. 13. Dorsal shield of type specimen of *Prolaspis (Cosmaspis) transversa*, n. subgen., n. sp., PF 4334 ($\times \frac{3}{4}$).

5215, 5221, 5233-4, 5237, 5243, 5252, 5259, 5260; branchial plates, PF 4382, 4384, 5300, 5307, 5311, 5315-6, 5319, 5324; dorsal spine, PF 5349; more or less articulated specimens, PF 4389 (fig. 17), 4390-1; juvenile articulated or associated specimens, PF 4490, 4492, 4494, 4496, 4953, 4969.

Occurrence.—Lower Devonian, Beartooth Butte formation, Cottonwood Canyon, east of Lovell, NE $\frac{1}{4}$, sec. 4, T56N, R93W, Big-horn County, Wyoming.

Diagnosis.—As for genus. Dorsal shield attaining a length of 140 millimeters.

Description.—The ornament of bands of cross ridges is particularly characteristic of the subgenus *Cosmaspis*. In *P. (C.) transversa*

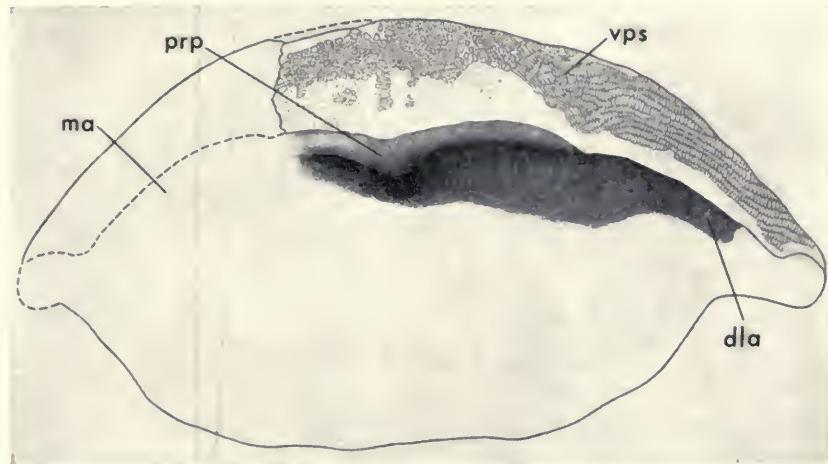


FIG. 14. Rostral plate of *Protaspis (Cosmaspis) transversa*, n. sp., ventral view, PF 5281 (about $\times 2$). *dla*, ventral surface of dorsal lamina; *ma*, matrix; *prp*, median preoral wall; *vps*, ventral preoral surface.

(fig. 7E) the individual cross ridges are more commonly arranged diagonally than transversely within the bands, and are typically gently convex and smooth-topped with crenulate margins. The bands are approximately 1.5 to 2.5 millimeters wide, while the individual ridges within the bands are 4.5 to 5.5 per millimeter. In the central or juvenile area of the dorsal disc the ornament is different and resembles that of typical pteraspids, for the ridges are not arranged in bands, but are concentric and parallel to lines of growth. They are finer, 6 to 8 per millimeter, and where unworn are sharp-crested or tuberculate. Outside of this zone is an intermediate zone where the ridges may occur diagonally in bands, where they are of intermediate coarseness, and where they grade from tuberculate into smooth crests.

The rostrum, though variable in proportions, may be described as of moderate length ($RL/TL=0.20$ to 0.27), broad ($RW/RL=1.75$ to 2.38), and broadly rounded anteriorly. Ventrally, it has a narrow preoral surface (fig. 14, *vps*) covered with irregularly-shaped, serrate tubercles, arranged in patches posteriorly, irregularly anteriorly, and in rows laterally. Dorsally, the posterior border of the rostral plate is usually (though not in the type) deeply indented at each side to receive the prominent anterior process of each orbital plate. Beneath each orbital plate there may be a separate suborbital

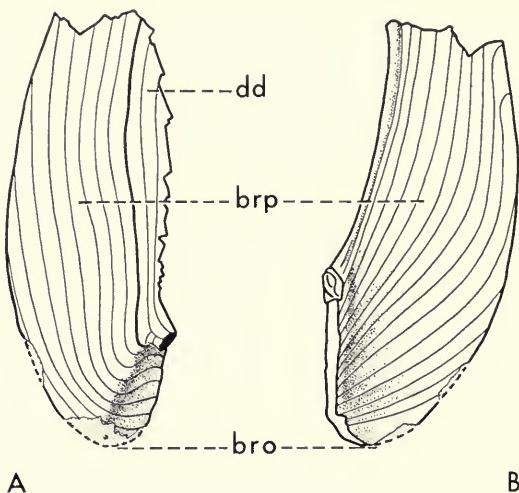


FIG. 15. Region of branchial opening of *Protaspis (Cosmaspis) transversa*, n. sp., PF 4352 ($\times 1\frac{1}{4}$). A, dorsal view; B, ventral view. *bro*, branchial opening; *brp*, branchial plate; *dd*, dorsal disc.

plate separating the rostral and branchial plates (PF 4334, 4338, 4775); in others (PF 4391, 4924) this space is occupied by a ventral process of the orbital plate. The pineal and orbital plates may or may not contact each other. The dorsal spine is long, projecting, and recumbent.

Each branchial plate extends a short distance behind the postero-lateral corner of the dorsal disc. In this region, the medial side of its dorsal lamina (fig. 15A) bends down to meet the inner margin of its ventral lamina (fig. 15B), and so surrounds the branchial duct, which opens at the posterior end of the branchial plate. The branchial duct extends forward from here for some distance in a deep groove between the dorsal and ventral laminae of the branchial plate. For a short distance anterior to the point where the branchial plate joins the dorsal disc, the branchial duct is bounded medially by one or more plates of thick, spongy bone, extending from the lateral margin of the dorsal disc to the medial margin of the ventral lamina of the branchial plate (fig. 16, ?*co*). This plate or plates has much of the relations of the cornual plate of *Protaspis arnelli*, as figured by Brotzen (1936, fig. 3:I), and may be called by that name provisionally.

One large articulated specimen, PF 4389, is crushed but shows much of the structure of the oral region and tail. At least 18 oral plates (fig. 17, *op*) are exposed but considerations of symmetry indi-

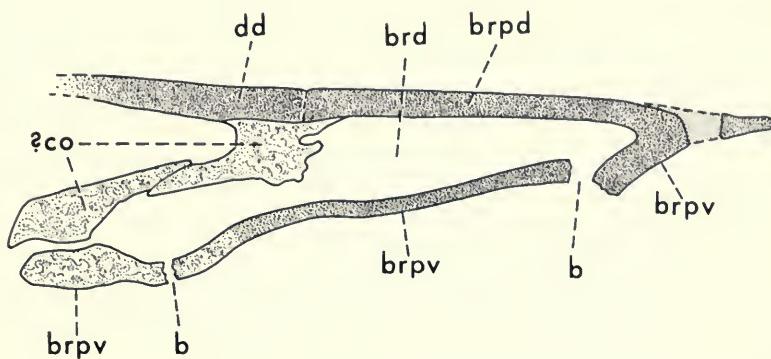


FIG. 16. Oblique section through left branchial duct of *Protaspis (Cosmaspis) transversa*, n. sp., PF 4334. *b*, breaks; *brd*, branchial duct; *brpd*, dorsal lamina of branchial plate; *brpv*, ventral lamina of branchial plate; *? co*, possible cornual plate; *dd*, dorsal disc.

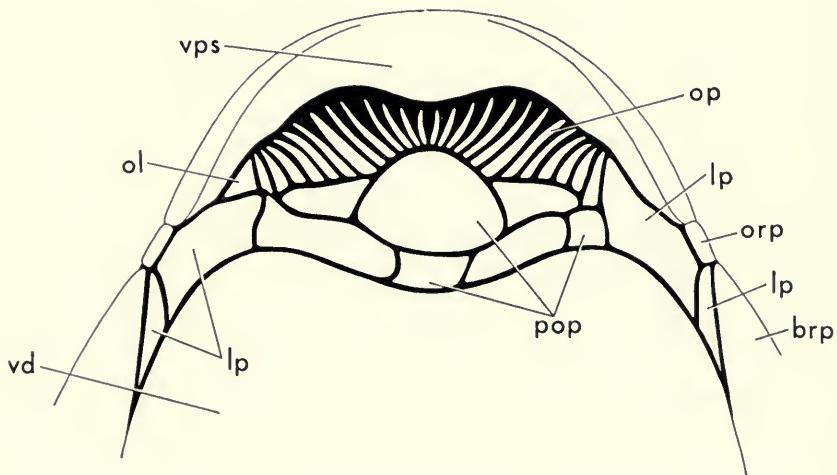


FIG. 17. Attempted restoration of the oral region of *Protaspis (Cosmaspis) transversa*, n. sp., ventral view, based on PF 4389 (about $\times 1$). *brp*, branchial plate; *lp*, lateral plates; *ol*, oral-lateral plate; *op*, oral plates; *orp*, orbital plate; *pop*, postoral plates; *vd*, ventral disc; *vps*, ventral preoral surface.

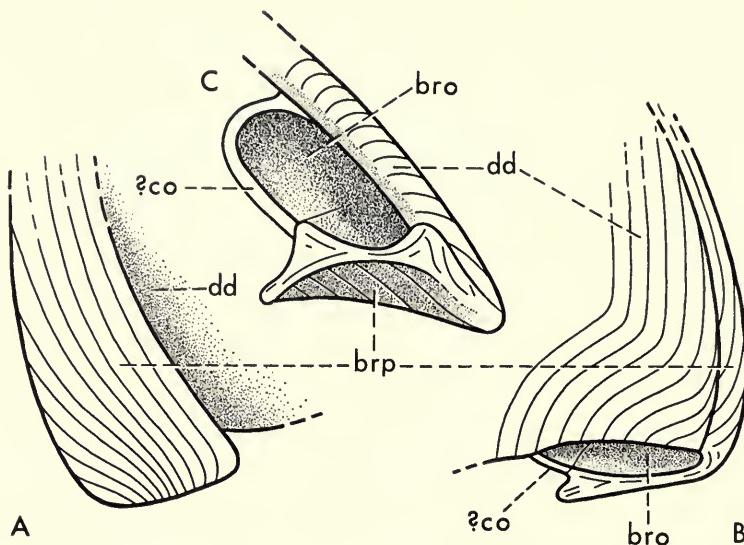


FIG. 18. Region of branchial opening of *Protaspis (Eucyclaspis) erroli* Denison, somewhat restored from PF 3814 (about $\times 2\frac{1}{2}$). A, ventral view; B, dorsal view; C, posterior view. *bro*, branchial opening; *brp*, branchial plate; *?co*, possible cornual plate; *dd*, dorsal disc.

cate that there were more originally. Between them and the ventral disc are two rows of postoral plates (fig. 17, *pop*). The posterior row bounding the ventral disc consists of a small median plate with one or two elongate plates bounding it on either side. The anterior row consists of a large, subtriangular median element with a small plate at either side. At each antero-lateral corner of the ventral disc are two lateral plates (fig. 17, *lp*).

The posterior and dorsal part of the tail is not preserved. The median ventral edge is formed by a series of ridge scales, of which the first is very large, the second even larger, while those behind gradually decrease in size posteriorly. The flank scales are also relatively large anteriorly and of the usual shape found in pteraspids.

As indicated above (p. 14), *Protaspis (Protaspis) mcgrewi*, though distinguished subgenerically from *Protaspis (Cosmaspis) transversa*, was surely closely related. *P. mcgrewi* rarely and locally shows bands of diagonal or transverse ridges, and agrees well in many other characters.

Protaspis (Cosmaspis) sp.

Protaspis sp., representing an undescribed subgenus, Denison, 1953, Fieldiana: Geol., 11, p. 350, fig. 84A.

Occurrence.—Lower Devonian, Card member of Water Canyon formation, Cache County, Utah.

Discussion.—The few fragments from the Water Canyon formation described by me in 1953 can now be referred to the subgenus

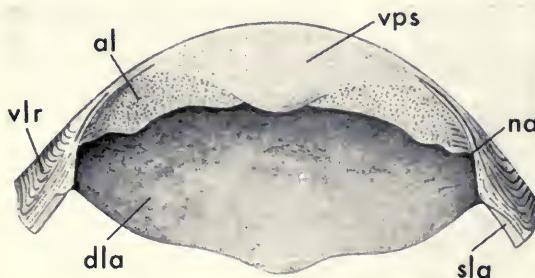


FIG. 19. Rostral plate of *Protaspis (Eucyclaspis) erroli* Denison, ventral view, restored from PF 3814 ($\times 2\frac{1}{4}$). *al*, ascending lamella; *dla*, ventral surface of dorsal lamina; *na*, possible narial notch; *sla*, sutural area for lateral plate; *vlr*, ventro-lateral face; *vps*, ventral preoral surface.

Cosmaspis. They differ from *P. (C.) transversa* in that the cross ridges within the bands of ornamentation are more regular and transverse and have flatter crests (fig. 7F). Also, the rostrum (PF 952) appears to be relatively longer.

Subgenus *Eucyclaspis*,¹ new subgenus

Type species.—*Protaspis (Protaspis) erroli* Denison.

Diagnosis.—A *Protaspis* in which the branchial ducts open posteriorly at the postero-lateral corners of the rather broad shield (fig. 18), and are bounded by the branchial plates ventrally and laterally, by the dorsal disc dorsally, and by probable cornual plates medially. The dorsal spine is slender and erect, and each orbital plate has a process projecting postero-laterally from its lateral margin behind the orbit. The ornament consists of very fine ridges more or less concentric to lines of growth.

Protaspis (Eucyclaspis) erroli Denison, 1967

Protaspis (Protaspis) erroli Denison, 1967, Jour. Linn. Soc. (Zool.), 47, pp. 34–37, text-figs. 1–2, pl. 1.

Occurrence.—Lower Devonian, near base of Grassy Flat member of Water Canyon formation, Logan Canyon, Cache County, Utah.

¹ From εὐκυκλός, well rounded; ασπίς, shield.

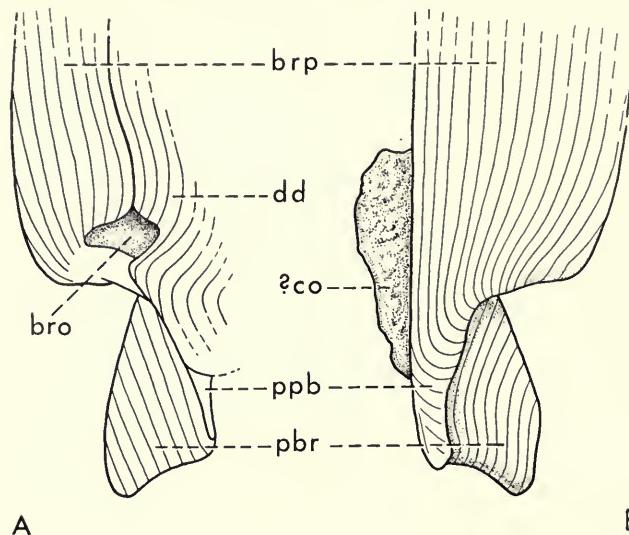


FIG. 20. Region of branchial opening of *Oreaspis dunklei*, n. gen., n. sp., slightly restored from U. S. Nat. Mus. 20524 (about $\times 3\frac{1}{2}$). A, dorsal view; B, ventral view. bro, branchial opening; brp, branchial plate; ?co, possible cornual plate; dd, dorsal disc; pbr, postbranchial plate; ppb, posterior process of branchial plate.

Diagnosis.—A small species with the median length of the dorsal shield attaining 61 millimeters. The rostral plate broad ($RW/RL=2.14$), bluntly rounded anteriorly, and with a narrow ventral preoral surface (fig. 19, vps). Ornament of sharp-crested, crenulate ridges, about 11 to 13 per millimeter.

Discussion.—This species differs from all the other species referred to the genus *Protaspis* in having projecting processes on the orbital plates, and from all except the species of *Gigantaspis* in its erect dorsal spine. These characters are considered sufficiently aberrant to warrant subgeneric separation.

Oreaspis,¹ new genus

Type species.—*Oreaspis dunklei*, new species.

Diagnosis.—Pteraspids with each branchial opening situated dorsally between the posterior part of the dorsal disc and branchial plate, and usually bounded posteriorly by both (fig. 20, bro). Typically a scale-like post-branchial plate (fig. 20, pbr) is attached to a posterior projection of each branchial plate. Dorsal shield moderately broad or vaulted.

¹ From *oπος*, mountain; *ασπις*, shield.

Oreaspis dunklei,¹ new species

Protaspis (Protaspis) cf. bucheri Denison, 1953, Fieldiana: Geol., 11, pp. 338-343, figs. 72, 77-79.

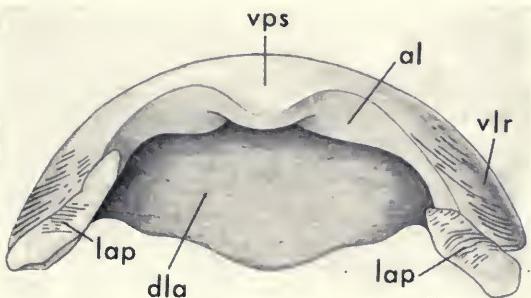


FIG. 21. Rostral and lateral plates of *Oreaspis dunklei*, n. sp., ventral view, somewhat restored from U. S. Nat. Mus. 20524 ($\times 2\frac{1}{4}$). *al*, ascending lamella; *dla*, ventral surface of dorsal lamina of rostral plate; *lap*, lateral plates; *vlr*, ventro-lateral face of rostral plate; *vps*, ventral preoral surface.

Type.—U. S. Nat. Mus. 20524, a dorsal shield lacking the postero-medial part (figs. 20-21).

Occurrence.—Lower Devonian, probably Card member of Water Canyon formation, Cottonwood Canyon, north of Logan Canyon, Cache County, Utah.

Diagnosis.—Rostrum short (RL/TL estimated to be 0.18) and broadly rounded anteriorly. Ornament rather coarse with about six flat-topped dentine ridges per millimeter. Total length of dorsal shield about 70 mm.

Discussion.—Though resembling *Protaspis* in the broad or vaulted dorsal shield and in the posterior position of the branchial openings, the distinctive relations of the branchial openings (fig. 20, *bro*) makes it convenient to distinguish this and related species as a separate genus. The rostrum is short and has a narrow ventral preoral surface (fig. 21, *vps*).

Oreaspis williamsi,² new species

Protaspis (Protaspis) dorfi Denison, 1953, Fieldiana: Geol., 11, pp. 337-338, figs. 75-76.

¹ After Dr. David H. Dunkle of the Natural Science Museum, Cleveland, Ohio.

² After Professor J. Stewart Williams of Utah State University, who has been active in the study of the Devonian rocks of northern Utah.

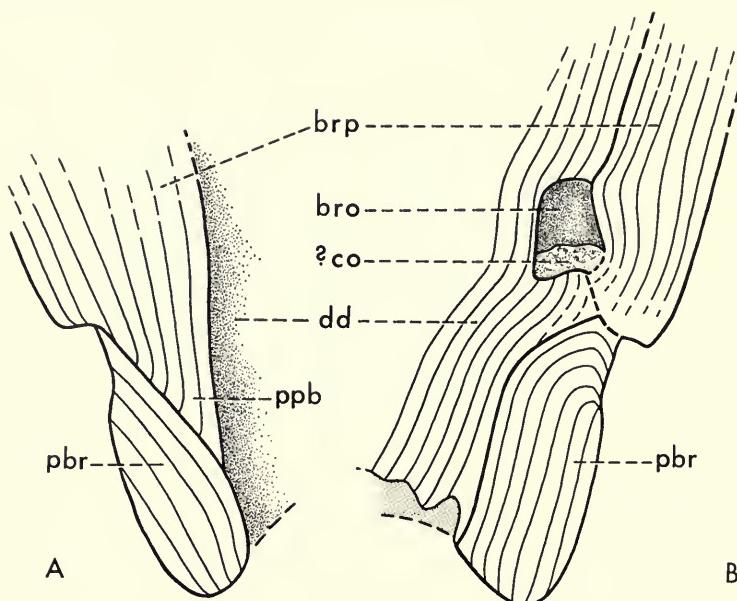


FIG. 22. Region of branchial opening of *Oreaspis williamsi*, n. sp., PF 868 ($\times 3$). A, ventral view; B, dorsal view. *bro*, branchial opening; *brp*, branchial plate; $?co$, possible cornual plate; *dd*, dorsal disc; *pbr*, postbranchial plate; *ppb*, posterior process of branchial plate.

Type.—Field Museum, PF 868, a flattened dorsal shield.

Occurrence.—Lower Devonian, Card member of Water Canyon formation, Blacksmith Fork, Cache County, Utah.

Diagnosis.—Rostrum short ($RL/TL=0.17$) and sharply rounded anteriorly. Ornamentation very fine with about nine dentine ridges per millimeter in the midline of the dorsal disc. Total length of dorsal shield 121 mm.

Discussion.—This species resembles *Protaspis dorfi* in the proportions and shape of its rostrum and in its fine ornamentation. In the structure of its branchial opening (fig. 22, *bro*) it is quite different from *P. dorfi*, which was inadequately known at the time of my 1953 paper, and in this respect is closely related to *Oreaspis dunklei*.

Oreaspis ampla (Bryant), 1933

Protaspis ampla Bryant, 1933, Proc. Amer. Phil. Soc., 72, pp. 299–300, text-fig. 3, pl. 10; 1935, Proc. Amer. Phil. Soc., 75, p. 123, pl. 14.

Protaspis nanus Bryant, 1933, Proc. Amer. Phil. Soc., 72, pp. 298–299, pl. 9, fig. 1.

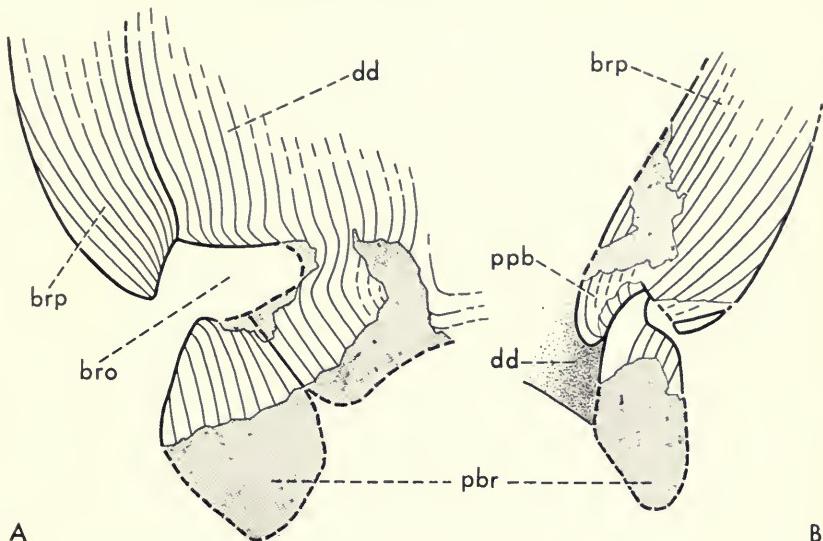


FIG. 23. Region of branchial opening of *Oreaspis ampla* (Bryant) ($\times 1\frac{1}{2}$). A, dorsal view, PF 2167; B, ventral view, PF 2166. bro, branchial opening; brp, branchial plate; dd, dorsal disc; pbr, postbranchial plate; ppb, posterior process of branchial plate.

Protaspis perlatus Bryant, 1933, Proc. Amer. Phil. Soc., 72, pp. 300-302, text-fig. 4, pl. 11.

Protaspis perryi Bryant, 1933, Proc. Amer. Phil. Soc., 72, pp. 302-303, pl. 12, figs. 1-2.

Protaspis amplus-perlatus-perryi group, Denison, 1953, Fieldiana: Geol., 11, p. 335.

Occurrence.—Lower Devonian, Beartooth Butte formation, Beartooth Butte, Park County, Wyoming.

Diagnosis.—Rostrum of moderate length, relatively longer in larger individuals ($RL/TL=0.23-0.32$) with the roundness of its anterior end intermediate between that of *O. dunklei* and *O. williamsi*. Ornament coarse, with about five dentine ridges per millimeter. Total length of dorsal shield reaching 170 mm.

Discussion.—In 1953 (p. 335) I considered Bryant's species, *Protaspis ampla*, *P. nanus*, *P. perlatus*, and *P. perryi*, to be closely related, and here I go one step further and place them in synonymy. This species differs from typical *Protaspis* in the structure of its gill openings, which resembles that of *Oreaspis dunklei*. A Field Museum specimen, PF 2166 (fig. 23B), shows this region in ventral view, and differs from *O. dunklei* and *O. williamsi* only in that the

posterior process of the branchial plate is relatively small, and the scale-like postbranchial plate relatively large. PF 2167 (fig. 23A) shows the dorsal side with the branchial opening in typical position, but it differs from *O. dunklei* and *O. williamsi* in that the branchial plate does not extend posteriorly to meet the dorsal disc and postbranchial plate posterior to the branchial opening. A specimen of *O. ampla* figured by Bryant (1935, pl. 14) appears to have the same structure.

? *Oreaspis* sp.

A few fragmentary specimens in the Field Museum collection from the Card member of the Water Canyon formation of Cache County, Utah, resemble *Oreaspis* in the position of their branchial openings; that is, they are near the posterior end of the branchial plates, but not terminal, and open dorsally between the branchial plates and dorsal disc. They differ from typical *Oreaspis* in lacking the posterior process on the branchial plate and the scale-like postbranchial plate. One such specimen (PF 869), figured by me in 1953 (fig. 73) as *Protaspis* sp., has a smooth, blunt posterior termination on the branchial plate, but two others (PF 875, 878) have a rough, concave termination to which a postbranchial plate might have attached. If this were so, the difference from typical *Oreaspis* would be minor.

*Lampraspis*¹, new genus

Type species.—*Lampraspis tuberculata*, new species.

Diagnosis.—Pteraspids with each branchial opening well in advance of the posterior corner of the dorsal shield, opening dorsally, bounded anteriorly and laterally by a branchial plate, posteriorly by a large posterior cornual plate, and medially by a small anterior cornual plate. Dorsal shield of moderate width, and in life well arched. The rostral plate short and broad with a narrow ventral preoral surface. Dentine ridges typically coarse and knobby, or subdivided into elongate tubercles.

Lampraspis tuberculata, new species

Type.—Field Museum, PF 4342, a dorsal shield (figs. 24, 25A).

Referred specimens.—Associated dorsal shield and ventral disc, PF 4754; dorsal shields, PF 4370, 4756, 4913 (fig. 7D), 4916, 4919, 4920, 4922, 4928, 5865; dorsal shields exposed ventrally, PF 4925

¹ From λαμπρός, splendid; ασπίς, shield.



FIG. 24. Dorsal shield of type specimen of *Lampraspis tuberculata*, n. gen., n. sp., PF 4342 ($\times \frac{3}{4}$).

(fig. 25B), 4927; parts of dorsal shields, PF 4341, 4351, 4761, 4767, 4771, 4941, 4943, 5350; incomplete, partly articulated juveniles, PF 4946, 4952, 4954-5; juvenile dorsal discs, PF 4371, 4373-4, 4393, 4400, 4407, 4417, 4432, 4436, 4776, 4972-3, 4976, 4980, 4982-3, 5019, 5046, 5064, 5068, 5078; juvenile ventral discs, PF 4141, 4440-1, 4445, 4448, 4455-7, 4459, 4462, 4464-5, 4467-8, 4470, 4479, 5023, 5095-6, 5099, 5103, 5105, 5107-8, 5111, 5116, 5118-9, 5125-9, 5131, 5134-6, 5138, 5150, 5154, 5162-3, 5170, 5172, 5174, 5182-3, 5188, 5190; larger ventral discs, PF 4366, 4784, 4786; rostral plates, PF 5261 (fig. 26), 5263, 5270-3, 5287, 5290, 5297; orbital plates, PF 5199, 5202, 5204, 5212, 5214, 5216-7, 5222, 5225, 5229, 5230-2, 5238-9, 5240, 5244-7, 5250, 5254-5; branchial plates, PF 4385, 5306, 5317-8, 5323.

Occurrence.—Lower Devonian, Beartooth Butte formation, Cottonwood Canyon, east of Lovell, NE $\frac{1}{4}$, sec. 4, T56N, R93W, Big-horn County, Wyoming.

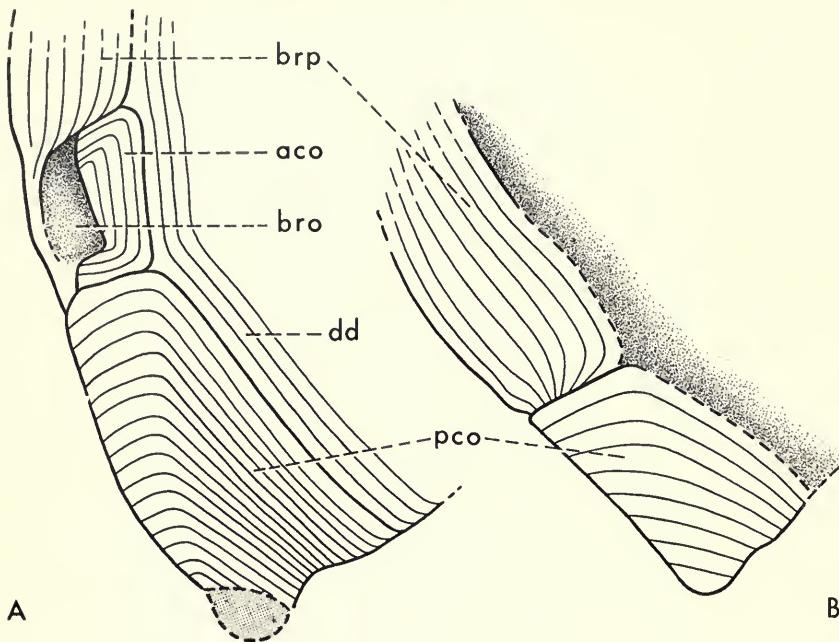


FIG. 25. Region of branchial opening of *Lampraspis tuberculata*, n. sp., somewhat restored ($\times 1\frac{1}{2}$). A, dorsal view, PF 4342; B, ventral view, PF 4925. *aco*, anterior cornual plate; *bro*, branchial opening; *brp*, branchial plate; *dd*, dorsal disc; *pco*, posterior cornual plate.

Diagnosis.—As for genus. Dorsal shield attaining a length of 118 mm.

Description and discussion.—At first glance, *Lampraspis*, with its broad (when flattened) dorsal shield, short broad rostrum, and small recumbent dorsal spine, would appear to be a typical *Protaspis*. However, the position of the branchial openings (fig. 25A, *bro*) far in advance of the postero-lateral corners of the dorsal shield distinguishes *Lampraspis* sharply from all *Protaspis* and *Oreaspis*, and suggests a relationship to *Pteraspis* or *Proptopteraspis*. In addition, the anterior and posterior cornual plates (fig. 25, *aco*, *pco*), except for the large size of the latter, together have precisely the relationships of the typical single cornual plates of *Pteraspis*. However, two juvenile specimens reveal an interesting situation. The larger of these, PF 4952, whose dorsal shield may have been about 60 mm. long, has small scale-like posterior cornuals, and the branchial openings occupy a much more posterior position than they do in adults. The smaller juvenile, PF 4955, whose dorsal shield was probably about 30 mm.

long, has the branchial openings nearly at the postero-lateral corners of the shield, and the posterior cornuals as seen in ventral view are minute plates, 3 mm. long, projecting somewhat at the corners of the shield. These two specimens suggest that *Lampraspis* was derived from a *Protaspis*-like pteraspid, and that the anterior position of the branchial openings is secondary phylogenetically as well as ontogenetically.

The ornamentation of *Lampraspis* (fig. 7D) consists characteristically of coarse knobby ridges, with crenulate margins basally, about five to six per millimeter. Locally, and especially in certain areas such as the branchial and posterior cornual plates, the ridges appear to be subdivided into elongate tubercles, much like those of *Cyrtaspidichthys*; in some cases, however, these tubercles are united at their bases into a ridge. Near the center of growth of the dorsal disc the juvenile ridges, where unworn, may be nearly as coarse and knobby as more peripheral ridges. In PF 4913 the juvenile ridges are slightly finer, and most centrally have a continuous crest without knobs.

The dorsal shields of *L. tuberculata* are almost invariably flattened, which makes them appear quite broad. However, the ventral discs assigned to this species are of moderate proportions; for example, the ventral disc on PF 4754 has a width/length ratio of 0.73. This means that the apparent breadth of the associated dorsal shield is the result of flattening, and in life it must have been narrower and highly vaulted. The rostra are usually crushed or flattened so the

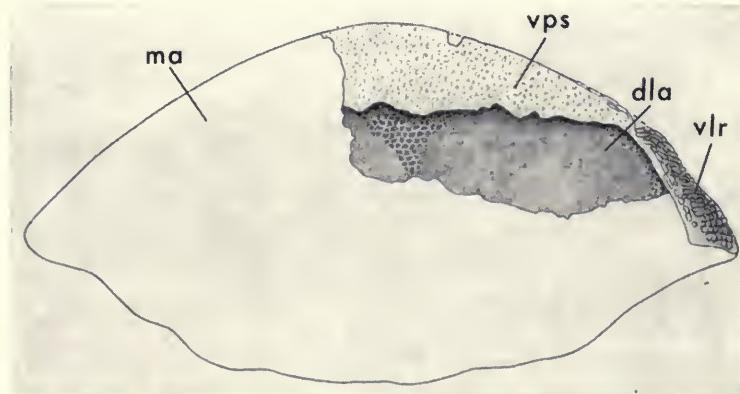


FIG. 26. Rostral plate of *Lampraspis tuberculata*, n. sp., ventral view, PF 5261 ($\times 3$). *dla*, ventral surface of dorsal lamina, lacking the basal layer anteriorly; *ma*, matrix; *vlr*, ventro-lateral face; *vps*, ventral preoral surface.

ratios of their width/length are unreliable. However, the rostral plate is relatively short ($RL/TL=0.19-0.22$), broad, and bluntly or even squarely rounded anteriorly. As is to be expected in a short rostrum, the ventral preoral surface (fig. 26, *vps*) is narrow, and has a slight median posterior projection. This surface is mostly covered with a fine reticular ornamentation, but anteriorly there are fine tubercles. The pineal plate usually contacts the orbitals, though not in PF 4754. The orbital plates have a ventral process that separates the rostral and branchial plates. The dorsal spine is short and re-cumbent, and projects behind the dorsal disc in most, though not in all specimens.

Psephaspis Ørvig, 1961

Type species.—*Psephaspis williamsi* Ørvig.

Diagnosis.—Moderate to large-sized pteraspids with the shield usually relatively broad, and with the ornament consisting typically of denticles with crenulate margins. The branchial openings are at the postero-lateral corners of the shield, at the posterior ends of the branchial plates.

Discussion.—*Psephaspis* was originally referred to the Drepanaspida by Ørvig (1961, pp. 526–533), but was shown to be a pteraspid by me in 1968 (p. 270). Its known characters indicate a close relationship to *Protaspis*, from which it is most clearly distinguished by its psammosteid-like ornamentation. Additional differences may be discovered when it is more completely known. It is the latest pteraspid, and the only genus of the family known to survive into the Middle Devonian.

Psephaspis williamsi Ørvig, 1961

Psephaspis williamsi Ørvig, 1961, Ark. Zool., ser. 2, 12, nr. 33, pp. 526–533, figs. 6–10; Denison, 1968, Fieldiana: Geol., 16, p. 270, figs. 2, 7A.

Occurrence.—? Lower Devonian, upper part of Water Canyon formation, Cache County, Utah, and Bear Lake County, Idaho.

Diagnosis.—A species attaining a large size, and with the denticles lower and less convex than in *P. idahoensis*.

Psephaspis idahoensis Denison, 1968

Psephaspis idahoensis Denison, 1968, Fieldiana: Geol. 16, pp. 270–279, figs. 1, 3, 7B, 8.

Occurrence.—Middle Devonian, basal unit of Jefferson formation, Lemhi County, Idaho.

Diagnosis.—A species attaining a smaller size, and having higher, more convex denticles than *P. williamsi*.

Subfamily Doryaspidae

Rostral plate truncate anteriorly, and the mouth opening antero-dorsally between it and an elongate pseudorostrum, which is attached to the ventral shield.

Doryaspis White, 1935

Type species.—*Scaphaspis nathorsti* Lankester.

Dyreaspis A. Heintz, 1934, NATUREN, 58, p. 244 (*nomen nudum*); 1935, ANN. REPT. SMITHSONIAN INST., 1934, p. 235 (*nomen nudum*).

Doryaspis White, 1935, PHIL. TRANS. ROY. SOC. LONDON (B), 225, p. 444; FØYN AND HEINTZ, 1943, SKR. NORGES SVALBARD-OG ISHAVS-UNDERSØK., 85, PP. 14-15; OBRUCHEV, 1964, OSNOVY PALEONTOLOGII, 11, p. 69.

Lyktaspis N. Heintz, 1968, PROC. 4TH NOBEL SYMP., STOCKHOLM, 1967, p. 73.

Diagnosis.—An aberrant pteraspid with the rostral plate short and truncate anteriorly, and underlain by a long pseudorostrum attached to the ventral shield, and with the mouth opening antero-dorsally between the rostrum and pseudorostrum. The cornual plates project far laterally. The ornament consists of concentric ridges subdivided by a system of radiating grooves.

Doryaspis nathorsti (Lankester)

Scaphaspis nathorsti Lankester, 1884, K. Svenska Vetenskapsakad. Handl. (n.f.), 20, no. 9, p. 5, pl. 1, figs. 1-3.

Pteraspis nathorsti Woodward, 1891, Ann. Mag. Nat. Hist., (6), 8, p. 2, pl. 2, fig. 1.

Doryaspis nathorsti White, 1935, Phil. Trans. Roy. Soc. London, (B), 225, p. 444, text-fig. 80, pl. 25, fig. 102; FØYN AND HEINTZ, 1943, SKR. NORGES SVALBARD-OG ISHAVS-UNDERSØK., 85, p. 14, fig. 5A; OBRUCHEV, 1964, OSNOVY PALEONTOLOGII, 11, p. 69, fig. 44.

Lyktaspis nathorsti N. Heintz, 1968, PROC. 4TH NOBEL SYMP., STOCKHOLM, 1967, pp. 73-79, figs. 1-4.

Occurrence.—Lower Devonian, Lykta Division, Wood Bay Series, Spitsbergen.

Discussion.—According to Errol White (in litt., July 2, 1968), *Doryaspis* Dejean 1835 (Coleoptera) is a *nomen nudum*, as are its three species, which apparently have never been validated, so *Doryaspis* was available when used by White, in 1935. This being the

case, the new name, *Lyktaspis*, proposed by N. Heintz, was not necessary.

Doryaspis is an aberrant genus and occupies an isolated position with relation to other pteraspids. This has been recognized by Tarlo (1962, p. 265) who placed it in a separate family, Doryaspidae, and in a separate order, Doryaspida; by Obruchev (1964, p. 69) who used the family Doryaspidae; and by N. Heintz (1968, p. 79) who used the family Lyktaspidae, and with reservations the sub-order Lyktaspida. In my own work with Heterostraci I have not felt the need, as have some students of the group, to elevate families to orders and to create new families, but have found that retaining the original family rank and using subfamily divisions has been adequate to express the grouping and relationships of genera. Using this approach, *Doryaspis* can be placed in a subfamily, Doryaspidae, to distinguish it from all other pteraspids, which have been referred to the Pteraspidae.

Pteraspidae incertae sedis

Two small pteraspids from the Lower Devonian, Wood Bay Series, of Spitsbergen have been described by Natascha Heintz (1960) as *Pteraspis* ? *lyktenensis* and *Pteraspis* ? *minor*. They are known only from isolated dorsal and ventral discs, and are distinguished particularly by the following: their coarse, non-crenulated dentine ridges; the absence of a dorsal spine; the fact that the median longitudinal sensory canals meet a loop of the supraorbital (or pineal) canals on the dorsal disc; and the inclusion of the lateral longitudinal sensory canals on dorsal discs as small as 14 and 18 millimeters. The inclusion of the lateral sensory canals is no proof that these discs belonged to adults, for many pteraspids continue to grow long after this stage, as has been clearly shown by White (1958, p. 230, figs. 4-8). However, the inclusion at such a small size indicates that the adults were small, and the extension of the supraorbital canals onto the dorsal disc is known only in small pteraspids. *Pteraspis* ? *lyktenensis* has been referred to a new genus, *Grumantaspis*, by Obruchev (1964, p. 69), and *Pteraspis* ? *minor* has placed in another new genus, *Ennosveaspis*, by Stensiö (1964, p. 363). What little is known about them hardly warrants their separation into two distinct genera, in fact, at present they are inadequately characterized generically. They may represent persistently primitive pteraspids, as suggested by N. Heintz (1960, p. 11).

Pteraspis dixoni White (1938, pp. 100-110, figs. 11-25) was referred to a new genus *Penygaspis*, by Stensiö (1958, p. 292) because of a presumably different manner of growth, as inferred from its dentine ridge pattern. The distinction of its ridge pattern is that the central areas of the dorsal and ventral discs have more or less longitudinal ridges, while only the peripheral parts have the usual concentrically arranged ridges. Stensiö was probably correct in assuming that the central areas were mineralized at one time (synchonomorally), but this is also true of pteraspids with concentric central ridges, as will be shown later. One difference is that the central areas are relatively large, with a length on the order of 25 millimeters. The longitudinal arrangement of the central ridges is known to occur occasionally in other pteraspids, such as *Protaspis (Europrotaspis) crenulata* White (1961, pp. 277-278, pl. 43, fig. 4), and may be considered a relic of cyathaspid ancestry. Until this species is more completely known it must remain *incertae sedis*, but it is probably primitive.

Protaspis (Protaspis) tenuistriatus Denison (1953, pp. 343-348, figs. 80-81) does not preserve the posterior part of the shield, so the position of the external branchial openings is uncertain. The slight development of the branchial groove in the most posterior preserved part of the left branchial plate suggests that the branchial openings were posterior, but there is no way to tell whether they are the type found in *Protaspis* or in *Oreaspis*.

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